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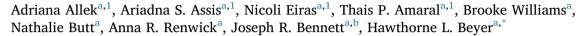
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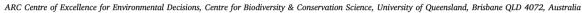
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The threats endangering Australia's at-risk fauna





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ABSTRACT

Reducing the rate of species extinctions is one of the great challenges of our time. Understanding patterns in the distribution and frequency of both threatened species and the threatening processes affecting them improves our ability to mitigate threats and prioritize management actions. In this quantitative synthesis of processes threatening Australian at-risk fauna, we find that species are impacted by a median of six threats (range 1–19), though there is considerable variation in numbers of threats among major taxonomic groups. Invasive species, habitat loss, biological resource use, natural systems modification and climate change are the processes most commonly affecting Australian threatened species. We identified an uneven distribution of research knowledge among species, with half of the total number of species-specific peer-reviewed scientific publications associated with only 11 threatened species (2.7%). Furthermore, the number of threats associated with each species was correlated with the research effort for that species, and research effort was correlated with body mass. Hence, there appears to be a research bias towards larger-bodied species, and certain charismatic species, that could result in inferences biased towards these favored species. However, after accounting for these effects we found that for birds, amphibians, reptiles and marine mammals body mass is positively correlated with the number of threats associated with each species. Many threats also co-occur, indicating that threat syndromes may be common.

1. Introduction

Biodiversity is threatened by many factors, and is currently in crisis on a global scale despite worldwide conservation efforts (Butchart et al., 2010). Processes driving species declines are affecting ecosystem services on which humans depend and are also leading to species extinction rates up to 100–1000 times higher than background rates (Pimm et al., 2014; Ceballos et al., 2015). Moreover, the number of threatened species at risk of extinction far exceeds resources available for conservation, which inevitably leads to some species being prioritized over others (Bottrill et al., 2008). This prioritization process can be usefully informed by understanding the link between threats and extinction vulnerability (Myers et al., 2000): assessing species' vulnerability to threats is part of an integrated scientific framework for establishing priorities and conservation plans (Margules and Pressey, 2000; Pressey et al., 2007).

Developing an understanding of the link between threatening processes (henceforth 'threats') and extinction risk is useful for more than one reason. First, synergies and feedbacks among threats may increase risk of extinction (Myers, 1987; Brook et al., 2008; Laurance and

Useche, 2009; Doherty et al., 2015). Identifying such synergies is important for both quantifying the risk of extinction and for prioritizing threat mitigation. Second, it may be inefficient to base conservation prioritization on an evaluation of species and threats that are assumed to be independent as this may fail to account for possible efficiency gains that could be achieved by addressing threats affecting multiple species. There may be, for example, economies of scale that can be achieved when mitigating a threat at large spatial scales (e.g. national scales), perhaps through legislative change or the development of incentive programs. Threat mitigation in an area may also benefit more than one species (e.g. reduction of feral cat and fox densities may benefit several species; Dexter and Murray, 2009). Or there may simply be cost-efficiencies resulting from sharing of infrastructure or implementation costs among several species occurring in the same area. Third, resolving some threats may require strong cross-jurisdictional cooperation, which can be facilitated by explicitly identifying the threats that can be most effectively addressed cooperatively (Kark et al., 2015). Thus, there are several ways in which considering the distribution and frequency of threats among all threatened species can improve conservation prioritization.

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A comparative approach to threat analysis may also provide useful insight into taxonomic and life history related patterns of association between threats and threatened species. Such patterns could inform a stronger mechanistic understanding of how threat mitigation may lead to a reduction in extinction risk and the time frame over which that may happen, and could provide a basis for estimating the types and impacts of threats affecting species that have not yet been assessed. Species characteristics such as body mass and generation time are often correlated with population viability and extinction risk (Jennings et al., 1998; Purvis et al., 2000; Fisher and Owens, 2004; O'Grady et al., 2004; Cardillo et al., 2005), although the associations between such characteristics and threats are not currently well understood. Given that the ultimate goal of management and conservation is to ensure the longterm persistence of species, management has arguably already failed by the time a species becomes listed as threatened. In some cases, it is likely to be less costly and more feasible to mitigate threats and prevent further population declines before a species becomes threatened. Understanding the link between threats and extinction risk could, therefore, facilitate the identification of species that are likely to become threatened in the future and the processes that are likely to affect them.

Australia is one of 17 megadiverse countries (Lindenmayer et al., 2010), with many endemic species. Since European settlement, the rate of species extinction in Australia has been high; for example, mammal extinctions are the highest in the world, with > 10% of endemic terrestrial mammal species now lost (Woinarski et al., 2015). Given the urgency of the situation, we present a continental-scale quantitative synthesis of threat status and threats for Australian threatened fauna. We map spatial patterns in the distribution of threatened species and threats across Australia. We then develop a statistical model to identify predictors of the number of threats associated with each species to evaluate the following questions: (i) are there differences in the numbers of threats associated with each species among taxonomic groups and conservation status groups?; (ii) are larger mass species typically associated with greater numbers of threats?; and (iii) are more threats described for species associated with larger numbers of peer-reviewed scientific papers? We also evaluate whether threats typically co-occur versus whether the distribution of threats among species is random.

2. Methods

A total of 497 animal species and subspecies, including birds, mammals, fishes, frogs, reptiles, and invertebrates, are listed as threatened under the Australian Commonwealth Environmental Protection and Biodiversity Conservation Act 1999 (EPBC). For each of these species we compiled information on threats, threat status (EPBC and IUCN), 16 taxonomic and morphological characteristics, distribution and abundance characteristics and research effort. Specifically, information for each species included threat status, phylum, class or order (bird, mammal, fish, reptile, amphibian, invertebrate), adult body mass, body length, generation time, number of offspring, species range area, population size, number of subpopulations, lifespan, threats recorded in the EPBC and IUCN Red List listings, number of species-specific scientific publications, and geographical distribution (state/territory of occurrence). When measures of mass could not be found, mass was estimated on the basis of body length-mass relationships (Suppl. Mat. Figs. 1-3). This open access database has been published on the University of Queensland data repository (Allek et al., 2018).

Information from the EPBC list and the IUCN Red List provided the core of the database, supplemented with data from many other sources (peer-reviewed and grey literature, books, reports and other databases). Data were located using systematic searches of Thomson Reuters Web of Science and Google Scholar between November 2014 and August 2015. Some data for mammals were sourced from PanTHERIA (Jones et al., 2009), and for birds from the Action Plan for Australian Birds 2010 (Garnett et al., 2010) and the Australian Bird Data Version 1.0. Scientific Data (Garnett et al., 2015). The source of each entry is

recorded in the database and a complete description of each field is included in the database metadata (Allek et al., 2018). The number of species-specific peer-reviewed scientific publications was quantified using Web of Science by searching for the genus and species name of each species (in quotes) and retaining only research article and review document types.

Following the Salafsky et al. (2008) categorization, threats were divided into 11 broad types: 1. Urban and residential development; 2. Agriculture and aquaculture; 3. Energy production and mining; 4. Transportation and services corridors; 5. Biological resource use, which refers to consumptive use and harvest of wild populations; 6. Human intrusions and disturbance; 7. Natural system modifications; 8. Invasive and other problematic species and genes; 9. Pollution; 10. Geological events; and 11. Climate change and severe weather. Within each of these threat types, there are up to six subdivisions, with more detailed specifications of the threats (Suppl. Mat. Table 1). A key aim of this classification system is to identify the causes of processes that impact threatened species. Hence, there is no single habitat loss category in this system. Rather, habitat loss effects are attributed to the causes of habitat loss: usually either Urban and residential development (category 1) or Agriculture and aquaculture (category 2).

The Salafsky et al. (2008) categorization threat type 8, 'Invasive and other problematic species and genes' is here subdivided into three parts: 8.1. Invasive non-native/alien species; 8.2. Problematic native species; and 8.3. Introduced genetic material. In our database, to be more precise, and as it is especially relevant to Australia, we included three additional subcategories: 8.4. Invasive/non-native/alien pathogens; 8.5. Problematic native pathogens and; 8.6. Diseases - Unknown origin

Other threats that did not fit into any of the Salafsky et al. (2008) categories and were listed in the EPBC were found to be numerically rare and were omitted from our analysis. Only current and potential threats were classified and included in this database; past threats were omitted. Potential threats are defined as those that could jeopardize species persistence in the future and are recorded separately from current threats.

We used generalised linear models with Poisson distributed errors to identify predictors of the number of threats associated with each threatened species. We evaluated permutations (including interaction terms) of the covariates: body mass (natural log transformed), taxonomic group (mammals, fish, reptiles, birds, and amphibians), number of peer-reviewed published papers, and threat status (critically endangered, endangered, conservation dependent and vulnerable), under the condition that the taxonomic group factor was always required in the model. Competing models were ranked using Akaike information criteria (AIC; Suppl. Mat. Table 2).

To examine co-occurrence of threats among species, we used a fixed-equiprobable null model approach (cf. Gotelli and Ellison, 2002), whereby numbers of occurrences of each threat were held constant while individual occurrences among species were shuffled 10,000 times. Tail probabilities for the null hypothesis of 0.05 < P > 0.95 were determined as the frequency of randomized numbers of co-occurrences \leq or \geq the true number of co-occurrences (Gotelli, 2000). We tested patterns of threat co-occurrences among all species, and among taxonomic groups as per the analysis of threat predictors above.

3. Results

Threatened animal species are widely distributed across Australia with considerable regional variation in the relative proportion of major taxonomic groupings of species (Fig. 1a). Birds constitute the single largest proportion of threatened species in all areas except the Northern Territory, where mammals make up the largest proportion. Most taxonomic groups are represented in all areas with the exception of amphibians, which occur almost exclusively in Queensland, New South Wales and Victoria.

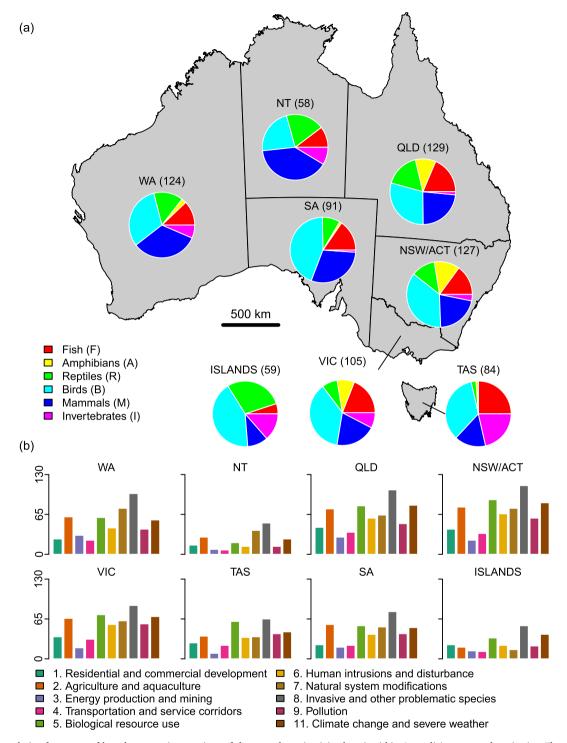


Fig. 1. (a) The relative frequency of broad taxonomic groupings of threatened species (pie charts) within Australia's states and territories. The total number of threatened species occurring within each area is noted in parentheses (a threatened species can occur in more than one area). Threatened species on remote islands, such as Christmas Island, are grouped into the "Islands" category. (b) Frequency distributions of major threat categories among all threatened species in each area. Rare threats, including geological events, are omitted.

Threats are also widely distributed across Australia (Fig. 1b). Threats associated with invasive and other problematic species (category 8) and habitat loss (categories 1 and 2 combined) are the most common across all areas, although biological resource use (category 5), natural system modification (category 7) and climate change and severe weather (category 11) are also prominent threats. Although threatened species are widely distributed in Australia, most species (59.6%) are found within a single state or territory (Suppl. Mat. Fig. 4).

Threats occurred at similar frequencies among critically endangered, endangered and vulnerable categories, but there was considerable variation in the frequency of threats among taxonomic groups (Fig. 2). The six conservation dependent species (all fish) were dominated by biological resource use threats (5), and marine mammals were commonly impacted by pollution (9). A breakdown of the frequency of the more detailed threats is presented in Suppl. Mat. Fig. 5. The least common threats included marine and freshwater aquaculture (2.4),

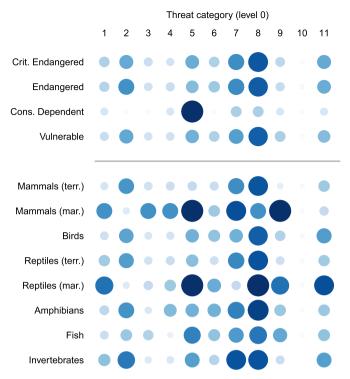


Fig. 2. Proportion of species in each conservation status category (top) or taxonomic grouping (bottom) that are associated with each of the major (level 0) threat types: (1) residential and commercial development, (2) agriculture and aquaculture, (3) energy production and mining, (4) transportation and service corridors, (5) biological resource use, (6) human intrusions and disturbance, (7) natural systems modifications, (8) invasive and other problematic species and genes, (9) pollution, (10) geological events, (11) climate change and severe weather. Darker shades and larger circles represent higher proportions of species (range 0–100%). For a finer breakdown of threats see Suppl. Mat. Fig. 6.

renewable energy (3.3), flight paths (4.4), war, civil unrest and military exercises (6.3), introduced genetic material (8.3), and geological events (10.1–10.3).

Relative to the total number of species in each taxonomic group, mammals had the highest proportion of species categorized as threatened (12.2%), followed by amphibians (10.7%) (Suppl. Mat. Fig. 6). Amphibians had the greatest proportion of species listed as critically endangered and endangered (1.9% and 5.2% respectively). Conversely, only 0.9% of all Australian fish species are listed, though sampling bias may account for much of the differences among major taxonomic groups.

Research effort, as quantified by the number of peer-reviewed papers associated with each threatened species, was not equal among species (Fig. 4). Of these publications, 50.7% were associated with only 2.7% of Australia's threatened species including the loggerhead turtle (Caretta caretta; n = 1857 publications), the green turtle (Chelonia mydas; n = 1843), the humpback whale (Megaptera novaeangliae; n = 817), the leatherback turtle (Dermochelys coriacea; n = 663), the southern elephant seal (Mirounga leonina; n = 573), the koala (Phascolarctos cinereus; n = 699), the fin whale (Balaenoptera physalus; n = 430), the hawksbill sea turtle (*Eretmochelys imbricata*; n = 378), the Kangaroo Island echidna (Tachyglossus aculeatus multiaculeatus, n = 372), the wandering albatross (*Diomedea exulans*, n = 333), and the great white shark (Carcharodon carcharias; n = 323). Conversely, the 323 (79.6%) least studied species account for only 10% of publications with 92 threatened species having no peer-reviewed scientific publications at the species level.

Publication bias, quantified as the proportional deviation from the expected number of publications if research effort was distributed

evenly among all listed species, was marked in some conservation status categories and taxonomic groupings (Fig. 5). Vulnerable species were typically more intensively studied than critically endangered and endangered species. Among listed species, there was strong positive bias towards marine mammals and marine reptiles, though the latter was driven largely by just three species of turtle (the loggerhead, green and leatherback turtles). There was bias against listed birds, terrestrial reptiles, amphibians and the 'other' group (primarily invertebrates).

At-risk species were associated with a median of six threats (range 1-19). The highest ranked model of the number of threats associated with each species included five covariates - body mass, taxonomic group, the number of peer-reviewed scientific papers and conservation status and an interaction between body mass and taxonomic group (Suppl. Mat. Table 2). Larger mass species were associated with a greater number of threats, with the exception of fish and terrestrial mammals (Table 1; Fig. 3). There was no evidence of a difference in number of threats associated with Vulnerable and Endangered species, but Critically Endangered and Conservation Dependent species had significantly fewer threats (Table 1). The number of peer-reviewed scientific papers for each species was positively correlated with the number of threats described for each species (Table 1) and with body mass (Suppl. Mat. Fig. 7). Overall, body mass explained 42.1% of the variation in number of peer-reviewed papers associated with each species. This varied among taxonomic groups as follows: reptiles (74.9%), amphibians (58.9%), terrestrial mammals (56.9%), birds (51.5%), fish (35.1%) and marine mammals (14.5%).

Pairwise co-occurrence of threats among all threatened species was common: 62% (28 of 45) threat pairs co-occurred more often than expected based on null expectations (Fig. 6). However, patterns of co-occurrence differed substantially among taxonomic groups (Suppl. Mat. Fig. 8).

4. Discussion

Australia is a megadiverse country and important for biodiversity globally (Lindenmayer et al., 2010). We present a synthesis of the conservation status of, and threats to, Australia's threatened species, describing the frequency and distribution of species and threats, and identifying considerable regional variation in both. Habitat loss has been identified as the most prevalent threat globally (Vié et al., 2009) and at national scales (e.g., the USA; Wilcove et al., 1998), although a recent analysis of over 8000 threatened or near-threatened species on the IUCN Red List reported that the greatest threat to biodiversity was biological resource use followed by agriculture (Maxwell et al., 2016). We found invasive species were the single most prevalent threat to Australian species. Within the global context, invasive species have previously been found to be the leading cause of extinctions in birds, and the second greatest cause of extinction in fish and mammals within the IUCN Red List species database (Clavero and Garcia-Berthou, 2005). However, the threat classification system we adopted is designed to identify ultimate drivers of threats (Salafsky et al., 2008). Habitat loss, which is caused by a variety of processes, is represented by several threat categories (residential and commercial development, agriculture, transportation corridors, etc.). Although none of these categories individually exceed the frequency of invasive species impacts, it is likely that, cumulatively, habitat loss rivals invasive species as the leading threatening process in Australia (Evans et al., 2011b).

Mammals had the highest proportion of threatened species among all the species groups considered, reflecting their sensitivity to invasive species (Woinarski et al., 2015). Terrestrial mammals across Australia have experienced high rates of extinction with > 10% of the 273 endemic terrestrial species becoming extinct over the last 200 years, and a further 21% now assessed as threatened (Woinarski et al., 2015). Most of these extinctions in Australia have been in remote, unmodified areas unaffected by habitat loss or development but instead subject to predation by introduced species, especially the feral cat and European red

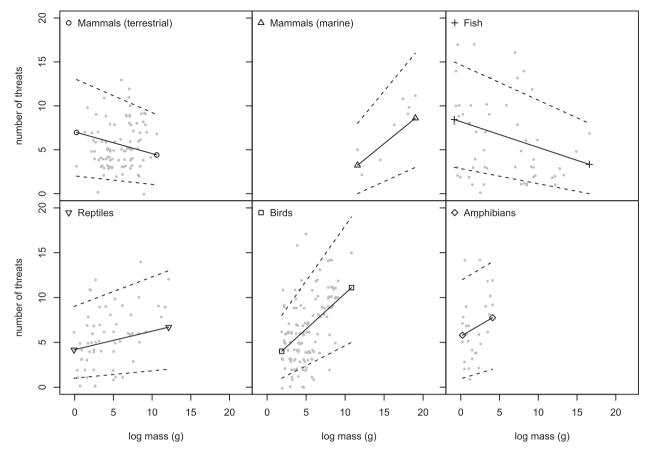


Fig. 3. Relationship between body mass (g, log scale, x axis) and the mean number of threats per species (y axis) quantified using a generalised linear model (axis scales are standardized across all plots). Lines are only plotted over the range of body mass values of species in each taxonomic group. Of the six major taxonomic groups all but fish and terrestrial mammals exhibit a positive correlation between body size and mean number of threats per species, though variation is considerable. Marine and terrestrial reptiles had overlapping mass distributions and similar trends with mass (-0.035 ± 0.063 SE and -0.050 ± 0.030 S.E. respectively), so were combined. Dashed lines are bootstrapped 95% confidence intervals, and the points represent the threatened species observations for each taxonomic group.

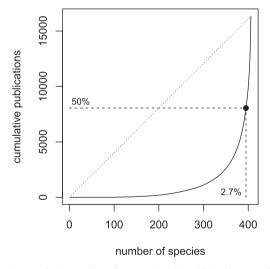


Fig. 4. The cumulative number of papers (y axis) published among all extant threatened species (x axis). If publication effort was evenly distributed among all species the distribution would follow the dotted line. The observed distribution (solid line) strongly deviates from the dotted line indicating an highly uneven distribution of publication effort. For example, only 2.7% of all species (11) account for 50% of all publications. Conversely, the 323 least studied species account for only 10% of all publications.

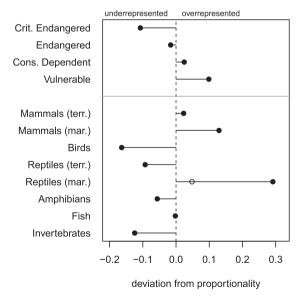


Fig. 5. Publication bias among conservation status and taxonomic groupings, as measured by the difference between the observed and expected number of publications if the total number of papers were distributed equally among all species. The open circle (•) is the representation of marine reptile publications after excluding loggerhead, green and leatherback turtles, which account for the majority of publications in that group.

Table 1

Parameter values for the top ranked model relating the number of threats associated with each threatened species (or subspecies) to body mass (g; log transformed), the taxonomic group, the number of peer-reviewed scientific papers (log transformed), and the conservation status. The reference categories for group and status were 'birds' and 'vulnerable' respectively, selected because they were the categories with the largest number of records.

	Estimate	Std. error	z value	Pr(> z)
(Intercept)	1.15	0.10	11.36	0.00
Mass	0.10	0.02	5.67	0.00
Group (fish)	0.80	0.12	6.45	0.00
Group (amphibian)	0.44	0.17	2.67	0.01
Group (mammal, marine)	-2.27	1.02	-2.23	0.03
Group (mammal, terrestrial)	0.35	0.16	2.18	0.03
Group (other)	0.59	0.32	1.81	0.07
Group (reptile)	0.28	0.14	2.05	0.04
Status (Conservation Dependent)	-1.20	0.31	-3.84	0.00
Status (Critically Endangered)	-0.16	0.08	-2.03	0.04
Status (Endangered)	0.04	0.04	0.87	0.38
Number papers	0.09	0.02	5.39	0.00
Mass:group (fish)	-0.15	0.02	-7.24	0.00
Mass:group (amphibian)	0.02	0.06	0.27	0.79
Mass:group (mammal, marine)	0.06	0.06	1.05	0.29
Mass:group (mammal, terrestrial)	-0.11	0.03	-4.19	0.00
Mass:group (other)	-0.06	0.06	-1.00	0.32
Mass:group (reptile)	-0.07	0.02	-2.99	0.00

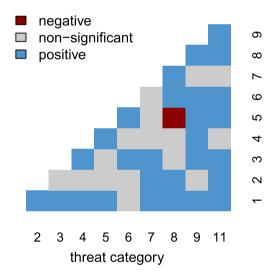


Fig. 6. This co-occurrence analysis identifies pairs of threatening processes that occur together more frequently ("positive") or less frequently ("negative") than expected based on a null model of random associations, among all Australian threatened fauna. The threat categories are: (1) residential and commercial development, (2) agriculture and aquaculture, (3) energy production and mining, (4) transportation and service corridors, (5) biological resource use, (6) human intrusions and disturbance, (7) natural systems modifications, (8) invasive and other problematic species and genes, (9) pollution and (11) climate change and severe weather. Rare threats are omitted. Co-occurrences by taxonomic group are presented in Suppl. Mat. Fig. 7.

fox (Woinarski et al., 2015). This is in contrast to North America where only one terrestrial mammal has become extinct since European settlement, and to other continents where the main cause of land mammal decline is habitat loss, hunting and human development (Woinarski et al., 2015).

Climate change and extreme weather presented a larger threat in the east of the country (Queensland, New South Wales and Victoria) than elsewhere, and amphibians, mostly occurring in this part of the country, are extremely sensitive to changes in temperature. Globally, 41% of amphibian species are listed in the IUCN Red List (IUCN, 2016). Reptiles are also intolerant of high temperatures (which can drive

changes in population sex ratios), and both groups are generally poor dispersers and are moisture dependent (Araújo et al., 2005; Deutsch et al., 2008). These traits drive vulnerability and increase the risk from threats. Furthermore, in Australia the high number of critically endangered and endangered amphibian species is also likely to be a reflection of the devastating impact of the invasive pathogen chytridiomycosis on many frog species (Stuart et al., 2004).

For birds, amphibians, reptiles and marine mammals body mass is positively correlated with the number of threats associated with each species. For terrestrial mammals, the weak negative correlation between body mass and threats may be a function of historical population declines in large mammals, as a result of human land use and land use change across Australia. Body size is less likely to be related to risk in regions with greater historical agricultural influence (Fritz et al., 2009). This human impact may have already worked to reduce the numbers of large mammals, and smaller mammals may therefore be at greater risk than larger species, due to facing different risks. For example, domestic cats or rats are likely to be a greater threat to smaller mammals than large. While the number of threats is not an indication of the severity of impact of threats, higher extinction rates occur in larger bodied species (Fisher and Owens, 2004). This may be a result of both environmental (e.g. larger geographic range increasing the likelihood of encountering a threatening process) and biological factors (e.g. low reproductive rates) putting these species at greater risk (Cardillo et al., 2005).

There is a complex relationship among body size, taxonomy, threats and research effort. Body mass is positively correlated with research effort, and research effort is positively correlated with the number of threats associated with each species. Any systematic bias against smaller species that contributes to a failure to identify the full suite of threats impacting them could have important implications for conservation and analyses of threat distribution and impact. The conservation status assigned to a species can have important implications for the level of protection and funding available to manage that species, and exposure to threats is one of several factors informing the listing process (Evans et al., 2016). Hence, research bias against small species could contribute to underestimation of the conservation status of those species, thereby reducing protection for those species.

In our analysis, five threat categories representing urban development, the energy industry, invasive species and pathogens, pollution and climate change, co-occurred with six or more other threat categories. In addition, human disturbance threats co-occurred significantly more often than expected with climate change and pollution, among all species and among all individual groups of terrestrial species. Interestingly, while threats co-occurred in most taxonomic groups, for fish and mammals, resource use and invasive species did not usually interact, and for mammals, human interference was the largest threat when they were free from invasive species pressure. Although co-occurrence of threats does not clearly indicate that there are synergistic effects among threats (i.e. the combined effect of two threats is greater than the additive effect of those threats separately), high levels of cooccurrence do indicate that this potential exists. More work is required to understand how threats may be organized into threat syndromes (collections of related threats) and to what degree threats may be synergistic.

Many threats span political boundaries and must be managed at scales larger than national, state or regional jurisdictions (Evans et al., 2016). Of the threatened species in Australia, 163 (31.4%) are found in more than one jurisdiction (state, territory or remote islands), and this needs to be accounted for in conservation plans. Landscape scale connectivity initiatives are now connecting states, territories, and different forms of tenure and governance across Australia (Wyborn, 2011). Establishing and maintaining these large scale, multi-stakeholder collaborations can be complex and strong governance and funding security are essential (Fitzsimons et al., 2013; Kark et al., 2015). Partners must share a common vision and the social and economic status of different landscapes and communities must be considered. Finally, research and

monitoring must underpin such initiatives to identify appropriate interventions and determine their success (Fitzsimons et al., 2013).

Understanding the patterns in the distribution, co-occurrence and frequency of processes threatening species may result in opportunities to improve the efficiency and efficacy of conservation management among many threatened species. There are several ways in which this might occur. First, efficiency can be improved by identifying potential economies of scale in the management of threats (Armsworth et al., 2011; Armsworth, 2014), particularly with respect to threats that are common, or widely distributed, or that impact many species. Efficiencies can arise through reductions in a number of costs, including acquisition costs (e.g. acquiring property rights), management costs (e.g. establishing and maintaining conservation activities on the site), transaction costs (e.g. administrative costs associated with finding and purchasing property), damage costs (e.g. offsetting agricultural losses arising from the species being protected), and opportunity costs associated with forgone gains that could have resulted from alternative uses of resources (Naidoo et al., 2006). Second, efficiency could be improved by explicitly identifying co-benefits and trade-offs in management actions that affect multiple species simultaneously (Adams et al., 2014). For example, Evans et al. (2011a) found that integrated threat management provided better return on investment than single-threat management and benefited multiple species. Issues of co-benefit and trade-offs are likely to become much more important and common as the number of threatened species increases, particularly in areas where there are concentrations of threatened species. Third, major long-term efficiencies in threatened species management may be achieved by prioritizing the mitigation of threats that are likely to result in the listing of further species in the future. In many cases prevention of species declines before they occur may be more cost-effective than mitigating and managing threatened species after they have become threatened (McCarthy et al., 2012). Intensively managing dominant (e.g. invasive species) and co-occurring (e.g. human disturbance and pollution) threats may help both currently-threatened species and those that may become listed in the future. Finally, coordinating with land management programs that are not specifically targeted at threatened species (e.g. fire management, revegetation projects) provide important new opportunities for mitigating threat (e.g. invasive species) impacts (Doherty et al., 2015).

We identified a clear disparity in scientific knowledge among species. Although the number of peer-reviewed publications is not a comprehensive measure of the knowledge of a species, and considerable species-specific information can be found in 'grey' literature such as government reports and recovery plans, it provides a reasonable relative quantification of the knowledge of a species. There is little coordination that aims to distribute research effort evenly among species (e.g. at the level of the Australian Research Council, the primary funding body of research in Australia). Moreover, species become listed at different times (Walsh et al., 2013), so an uneven distribution of knowledge does not necessarily indicate a failure in the funding process. Nevertheless, our analysis clearly demonstrates that some species receive a great deal more research attention than others and this creates opportunities to re-prioritize research funding allocations to address obvious gaps in knowledge (Martin-Lopez et al., 2009).

Conservation prioritization, the differential allocation of resources among species, is likely to improve conservation outcomes only if a minimum degree of understanding can be achieved across all species. Yet even basic ecological knowledge of the life history and population dynamics of many threatened species is lacking. The strong asymmetry in knowledge distribution among species may result in resources being preferentially allocated to species that we know more about (Martin-Lopez et al., 2009). These are often the charismatic species that attract most public interest (e.g. turtles, whales and koalas; see Results).

Threatened species lists such as the IUCN Red List or the EPBC, provide a formal, transparent procedure for assessing a species' risk of extinction (Rodrigues et al., 2006). The ranked threatened status

categories ('critically endangered', 'endangered', 'vulnerable', 'near threatened', 'least concern') provide a measure of the relative risk of extinction among assessed species. Threatened status per se may be of limited use for conservation prioritization because changes in status often reflect changes in the quality of information about a species rather than changes to the underlying ecology or extinction risk, confounding the interpretation of a change in status as a true change in extinction risk (Cuarón, 1993). There is also often severe taxonomic, geographical and politically motivated bias in the species that are assessed (Lamoreux et al., 2003; Walsh et al., 2013). Comprehensive assessment of birds, mammals, amphibians and other groups have been completed (Vié et al., 2009) whereas < 1% of invertebrates, and species overall, have been assessed (Baillie et al., 2004; Collen et al., 2012).

5. Conclusions

We argue that by explicitly considering the distribution and frequency with which threatening processes impact species we can identify new opportunities for improving conservation prioritization and the efficiency of management. We suggest that there are opportunities for benefiting from economies of scale, co-benefits from addressing threats common to many species, and avoidance of trade-offs when mitigating a threat may negatively impact other species of conservation concern (avoidance of perverse outcomes). However, the highly uneven distribution of knowledge among threatened species is concerning. The striking absence of peer-reviewed papers on numerous threatened species severely limits our ability to allocate conservation resources in an informed and rational manner. Any strategy to efficiently conserve Australian species must address this knowledge gap, or risk management decisions that are poorly informed, biased or both.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.03.029.

References

Adams, V.M., Alvarez-Romero, J.G., Carwardine, J., Cattarino, L., Hermoso, V., Kennard, M.J., Linke, S., Pressey, R.L., Stoeckl, N., 2014. Planning across freshwater and terrestrial realms: cobenefits and tradeoffs between conservation actions. Conserv. Lett. 7, 425–440.

Allek, A., Assis, A., Eiras, N., Amaral, T., Butt, N., Renwick, A., Bennett, J., Beyer, H., 2018. data from: Australia's threatened fauna and the threats they face. http://dx.doi. org/10.14264/uql.2018.255. https://espace.library.uq.edu.au/view/UQ:726491.

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513.

Armsworth, P.R., 2014. Inclusion of costs in conservation planning depends on limited datasets and hopeful assumptions. Year Ecol. Conserv. Biol. 1322, 61–76.

Armsworth, P.R., Cantú-Salazar, L., Parnell, M., Davies, Z.G., Stoneman, R., 2011.
Management costs for small protected areas and economies of scale in habitat conservation. Biol. Conserv. 144, 423–429.

Baillie, J., Hilton-Taylor, C., Stuart, S.N., 2004. 2004 IUCN Red List of Threatened Species: A Global Species Assessment. IUCN.

Bottrill, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C.N., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., et al., 2008. Is conservation triage just smart decision making? Trends Ecol. Evol. 23, 649–654.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., et al., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168.

- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253.
- Clavero, M., Garcia-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20 110–110.
- Collen, B., Böhm, M., Kemp, R., Baillie, J., 2012. Spineless: Status and Trends of the World's Invertebrates. Zoological Society of London, United Kingdom.
- Cuarón, A.D., 1993. Extinction rate estimates. Nature 366 118-118.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. U.S.A. 105, 6668–6672.
- Dexter, N., Murray, A., 2009. The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. Wildl. Res. 36, 252–261.
- Doherty, T.S., Dickman, C.R., Nimmo, D.G., Ritchie, E.G., 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. Biol. Conserv. 190, 60–68.
- Evans, D.M., Che-Castaldo, J.P., Crouse, D., Davis, F.W., Epanchin-Niell, R., Flather, C.H., Frohlich, R.K., Goble, D.D., Li, Y.W., Male, T.D., et al., 2016. Species recovery in the United States: increasing the effectiveness of the endangered species act. In: Issues in Ecology, Report Number 20. Ecological Society of America.
- Evans, M.C., Possingham, H.P., Wilson, K.A., 2011a. What to do in the face of multiple threats? Incorporating dependencies within a return on investment framework for conservation. Divers. Distrib. 17, 437–450.
- Evans, M.C., Watson, J.E.M., Fuller, R.A., Venter, O., Bennett, S.C., Marsack, P.R., Possingham, H.P., 2011b. The spatial distribution of threats to species in Australia. Bioscience 61, 281–289.
- Fisher, D.O., Owens, I.P.F., 2004. The comparative method in conservation biology. Trends Ecol. Evol. 19, 391–398.
- Fitzsimons, J., Pulsford, I., Wescott, G., 2013. Lessons from large-scale conservation networks in Australia. Parks 19, 115–125.
- Fritz, S.A., Bininda-Emonds, O.R.P., Purvis, A., 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecol. Lett. 12, 538–549.
- Garnett, S., Szabo, J., Dutson, G., 2010. The Action Plan for Australian Birds 2010. CSIRO Publishing.
- Garnett, S.T., Duursma, D.E., Ehmke, G., Guay, P.J., Stewart, A., Szabo, J.K., Weston, M.A., Bennett, S., Crowley, G.M., Drynan, D., et al., 2015. Biological, ecological, conservation and legal information for all species and subspecies of Australian bird. Sci. Data 2. 150061.
- Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. Ecology 81, 2606–2621.
- Gotelli, N.J., Ellison, A.M., 2002. Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. Ecology 83, 1604–1609.
- IUCN, 2016. IUCN Red List of Threatened Species.
- Jennings, S., Reynolds, J.D., Mills, S.C., 1998. Life history correlates of responses to fisheries exploitation. Proc. R. Soc. B Biol. Sci. 265, 333–339.
- Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., et al., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90 2648–2648.
- Kark, S., Tulloch, A., Gordon, A., Mazor, T., Bunnefeld, N., Levin, N., 2015. Cross-boundary collaboration: key to the conservation puzzle. Curr. Opin. Environ. Sustain. 12, 12–24.

- Lamoreux, J., Akcakaya, H.R., Bennun, L., Collar, N.J., Boitani, L., Brackett, D., Brautigam, A., Brooks, T.M., de Fonseca, G.A.B., Mittermeier, R.A., et al., 2003. Value of the IUCN red list. Trends Ecol. Evol. 18, 214–215.
- Laurance, W.F., Useche, D.C., 2009. Environmental synergisms and extinctions of tropical species. Conserv. Biol. 23, 1427–1437.
- Lindenmayer, D.B., Steffen, W., Burbidge, A.A., Hughes, L., Kitching, R.L., Musgrave, W., Smith, M.S., Werner, P.A., 2010. Conservation strategies in response to rapid climate change: Australia as a case study. Biol. Conserv. 143, 1587–1593.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253
- Martin-Lopez, B., Montes, C., Ramirez, L., Benayas, J., 2009. What drives policy decision-making related to species conservation? Biol. Conserv. 142, 1370–1380.
- Maxwell, S., Fuller, R.A., Brooks, T.M., Watson, J.E.M., 2016. The ravages of guns, nets and bulldozers. Nature 536, 143–145.
- McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., et al., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338, 946–949.
- Myers, N., 1987. The extinction spasm impending: synergisms at work. Conserv. Biol. 1, 14-21.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
- Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends Ecol. Evol. 21, 681–687.
- O'Grady, J.J., Reed, D.H., Brook, B.W., Frankham, R., 2004. What are the best correlates of predicted extinction risk? Biol. Conserv. 118, 513–520.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. Trends Ecol. Evol. 22, 583–592.
- Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. B Biol. Sci. 267, 1947–1952.
- Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., Brooks, T.M., 2006. The value of the IUCN Red List for conservation. Trends Ecol. Evol. 21, 71–76.
- Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C., Neugarten, R., Butchart, S.H.M., Collen, B., Cox, N., Master, L.L., O'Connor, S., et al., 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. Conserv. Biol. 22, 897–911.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1786.
- Vié, J.C., Hilton-Taylor, C., Stuart, S.N., 2009. Wildlife in a Changing World: An Analysis of the 2008 IUCN Red List of Threatened Species. IUCN.
- Walsh, J.C., Watson, J.E.M., Bottrill, M.C., Joseph, L.N., Possingham, H.P., 2013. Trends and biases in the listing and recovery planning for threatened species: an Australian case study. Oryx 47, 134–143.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. Bioscience 48, 607–615.
- Woinarski, J.C.Z., Burbidge, A.A., Harrison, P.L., 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proc. Natl. Acad. Sci. U.S.A. 112. 4531–4540.
- Wyborn, C., 2011. Landscape scale ecological connectivity: Australian survey and rehearsals. Pac. Conserv. Biol. 17, 121–131.